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# Female tannin avoidance: a possible explanation for habitat and dietary segregation of giraffes (*Giraffa camelopardalis peralta*) in Niger

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## Abstract

Niger is host to the last free-roaming herd of *G.c. peralta* (*Giraffa camelopardalis peralta*). We examined the foraging preferences of these giraffe in their dry-season habitats, with the goal of preserving the herd in the regions that they currently inhabit. The current dry-season habitat comprises two distinct vegetation zones. In both of these zones the giraffe must exist alongside the people of this region. The giraffes exhibit a sexual segregation in their dry-season habitat selection and forage choices. The females show a strong preference for the intermediate zone (IM) when lactating. The males and pregnant females show a preference for the Dallol Bosso (DB). Nursing cows exhibit an avoidance of tannins. Bulls and non-nursing cows prefer high protein and high fat forage, while subadults show a strong preference for high protein and carbohydrate contents and moderate tannin levels. *Combretum glutinosum* is the preferred species for adults of both sexes in the IM. Males and females have strong preferences for both *Acacia nilotica* and *Acacia seyal* in the DB. Sub-adults of both sexes strongly prefer *Prosopis africana* in the IM. Unlike females, males retain their preference for *A. nilotica* when in the IM.

**Key words:** foraging preference, giraffe, *G.c. peralta*, *Giraffa camelopardalis*, Niger, west African browsers.

## Résumé

Le Niger abrite la dernière population sauvage de *Giraffa camelopardalis peralta*. Nous avons étudié les préférences alimentaires de ces girafes dans leurs habitats de saison sèche, dans le but de maintenir cette population dans

les régions qu'elle occupe actuellement. L'habitat actuel de saison sèche comprend deux zones de végétation distinctes. Dans les deux zones, les girafes doivent cohabiter avec les gens de la région. Les girafes présentent une ségrégation sexuelle tant dans la sélection de l'habitat de saison sèche que dans les choix alimentaires. Les femelles allaitantes manifestent une forte préférence pour la zone intermédiaire (IM). Les mâles et les femelles pleines montrent une préférence pour le Dallol Bosso (DB). Les femelles qui s'occupent de jeunes évitent visiblement les tanins. Les mâles et les femelles sans jeune préfèrent un fourrage riche en protéines et en graisses, tandis que les subadultes manifestent une forte préférence pour un contenu élevé en protéines et en hydrates de carbone et des taux de tanins modérés. *Combretum glutinosum* est l'espèce préférée des adultes des deux sexes dans la IM. Les mâles et les femelles préfèrent nettement *Acacia nilotica* et *Acacia seyal* dans le DB. Les subadultes des deux sexes préfèrent nettement *Prosopis africana* dans la IM. Contrairement aux femelles, les mâles conservent leur préférence pour *A. nilotica* lorsqu'ils sont dans la IM.

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## Introduction

Niger is home to the last free-roaming herd of giraffes (*Giraffa camelopardalis peralta*) in west Africa and the last free-roaming herd of the race *peralta*. The herd in Niger decreased throughout the 1960s and 1970s. The severe droughts of the 1970s and 1980s in Niger helped to further degrade the landscape and decimate wildlife populations. Prior to the droughts, the giraffes were widespread and abundant in Niger (Ciofalo, 1995). After the droughts, the giraffes were forced into a small area surrounding the Kouré region and the Dallol Bosso, between Baléyara and Birnin Gaouré. While this defines

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the group's current range, some long distance movements by lone adults have been observed (Le Pendu & Ciofolo, 1999).

The giraffes now inhabit the Harikanassou region, where they were rarely seen before, and are now interacting regularly with humans. They are protected from hunting in Niger, where killing a giraffe is now a criminal offence. The region has no natural giraffe predators other than man, and only domestic herbivores as potential competitors. The occupancy of a new range, combined with the government's interest in developing ecotourism, inspired us to undertake a study of giraffes in the region. A dietary assessment of the herd was requested by Peace Corps Niger on behalf of the government of Niger. The preliminary questions we hoped to explore included: (i) Where were the giraffes living and what were they eating in their new range? (ii) Why had the giraffes settled in this region, and (iii) What, if anything, could be done to help ensure their continued presence?

## Methods

### *Study site*

The giraffes inhabit three vegetation zones in their core range. The core range is subdivided into dry season and wet season habitats. The dry season habitat is in the Kouré–Harikanassou region (termed the intermediate zone) and the Dallol Bosso. The average annual rainfall of between 400 mm and 500 mm defines this region as part of the Sahel. The herd is there from October to May, after which they congregate in the Kouré region following the first rains. The herd is widespread in the dry season habitat. We worked in the Harikanassou area, about 85 km south-east of Niamey, from January 1997 to February 1999.

The Dallol Bosso (DB) is an ancient riverbed with a shallow water table, as shallow as 0.5 m in the valleys and hollows. Many large, permanent waterholes and ponds also characterize this region. These ponds are often shallow (<1.5 m deep) and marshy. This zone is marked by comparatively fertile soils and an abundance of trees and tree species around the wetlands. The intermediate zone (IM) is more typical of the Sahel. It has sandy soils, scattered trees and low scrub brush. Most of the region is farmed in the rainy season and left fallow during the dry season. This area has a deep water table, often being as much as 50–60 m down.

### *Data collection*

Every giraffe was identified through a detailed photo log. The giraffes were photographed from both sides and assigned identification numbers at first sighting. When possible, the entire body, and in every instance the entire neck, was photographed. The original photo record was initiated by Peace Corps Volunteer Paul Peterson in 1995, revamped by PURNKO – a Dutch conservation organization – in 1996 and continued by our team. We also recorded pertinent information about the giraffes (i.e. sex, injuries, offspring, maternities, ages and deaths). The photographic record allowed us to determine the age of each giraffe for the duration of the study. Giraffes were designated as adults (>4 years old), subadults (between 18 months and 4 years old), juveniles (6–18 months old), and newborns (<6 months old). Their ages were determined based on known dates of birth or on the age of the individual at the first recorded sighting and/or photograph (some of which dated back to 1990). Foster (1966) first developed the concept of the photo-record. As he noted, coat patterns on giraffes do not change with age, and are unique to each individual.

The giraffes were tracked visually while driving Yamaha 125 cc dirt bikes. We selected the closest giraffe for focal animal observation, but tried not to sample the same animal more frequently than others in the herd. Each location where the giraffes were first encountered was recorded using a Grumman hand-held geographical positioning systems (GPS). Most of our observations were made during the early morning (07.00–11.00 h). We did not observe the giraffes eating after noon. They spent most of their time resting in the shade until early evening, presumably due to the high air temperatures, which often reached 49 °C. This was not true during the cold-season (late December–February), when the giraffes could be observed foraging until late afternoon. During each focal sample we recorded: (1) the species of each food item, (2) the height of each feeding bout, (3) the duration of each feeding bout in seconds, (4) which part of the plant was being taken, (5) the individual focal animal, and (6) the identity of all of the other giraffes present (modified from Young & Isbell, 1991).

To document the available vegetation, 20 plots were randomly selected from the entire study area. An additional five plots were each randomly selected from the Dallol Bosso (DB) and Intermediate Zone (IM). We selected an extra two plots in the IM which were frequented

**Table 1** Known chemical compositions of plants in the *G.c. peraltas*' dry-season habitat in Niger, from dry weight samples

	% Crude Protein	% Fats	% Crude Fibre	% Ash	% Moisture	% NFE	Source†	Tannin Content
<i>Acacia</i> species								
<i>A. nilotica</i>	12.9	5.1	13.7	1.1	52.0	32.2	(1)	Pods 30% <sup>(2)**</sup> Bark 20.0% <sup>(2)</sup>
<i>A. senegal</i>	28.6	3.0	16.2	0.4	61.0	19.8	(1)	
<i>A. seyal</i>	18.5	—	—	—	—	—	(2)	Pods 20% <sup>(2)</sup> Bark 20% <sup>(2)</sup> , 18–30% <sup>(5)</sup>
<i>Annona senegalensis</i>	8.2	—	—	—	10.5	—	(3)	
<i>Balanites aegyptica</i>	14.25	0.82	2.91	11.72	4.16	66.14	(4)	
<i>Combretum glutinosum</i>	10.0	1.02	1.82	14.15	5.04	67.97	(4)	
<i>Faibherbia albida</i>	13.63	0.77	2.15	12.75	3.88	66.82	(4)	Bark 20–28% <sup>(2)</sup>
<i>Guiera senegalensis</i>	13.13	0.18	1.55	11.46	4.06	69.62	(4)	
<i>Piliostigma reticulatum</i>	9.38	0.63	2.89	10.12	5.05	71.93	(4)	Bark 18% <sup>(2)</sup>
<i>Prosopis africana</i>	10.2	6.8	—	—	7.9	49.46	(3)	Bark 18% <sup>(2)</sup>
(seeds)	16.0–25.74	1.7–20.0	7.6–15.76	2.94–3.4	—	35.56–78.5	(5)	

\*All values apply to dry matter weight of leaves, unless otherwise noted.

—Denotes no available data for these values.

†Source citations: (1) Sauer (1983), (2) von Maydell (1983), (3) Irvine (1961), (4) Mohamed (1995), (5) Booth & Wickens (1988).

by the giraffes, resulting in a total of 32 sample plots. Each plot was 25 m in diameter (44.3 m<sup>2</sup>) (Barbour, Burk & Pitts, 1980). We recorded the frequency of each tree and shrub species within the plots (Dagg & Foster, 1976; Pellew, 1984).

### Data analysis

We defined the relative frequency of each tree or shrub species as the total number of stems per species divided by the total number of stems of all species detected in the surveys. In addition to the raw stem counts, we also calculated a weighted count for each species. This was intended to estimate the total value, i.e. the number and/or volume of leaves, of the sampled plants. We estimated the relative foraging effort by taking the total seconds that all giraffes were observed foraging at a tree species and dividing it by the total time all giraffes were observed foraging at all tree species.

The relative vegetation frequencies and the foraging data were used to establish a strength-of-preference variable (preference index). The preference index equalled the relative frequency of a plant species' occurrence subtracted from the giraffe's relative foraging effort (frequency) on that species. Thus, a rank of zero on the preference index scale indicated that a tree species was eaten at the same frequency with which it occurred in the

sample. A positive rank indicated a selective preference and a negative rank a selective avoidance of the species in question. Finally, the total amount of time the giraffes spent eating the various plant parts of each tree species was divided by the total amount of time spent by the giraffes eating that tree species. This represented the proportional dietary importance of each tree part to the giraffes.

Although sparse, information has been published on the chemical composition, including protein, ash, fat, fibre, moisture, carbohydrates (NFE) and tannin content of many species in these and similar habitats (Table 1). This table contains all the available information on the species eaten by giraffes in Niger.

## Results

### Herd composition and zone occurrence

By the end of the study period the herd comprised 18 adult males, 26 adult females, 12 subadult males, 6 subadult females, 4 juvenile males, 7 juvenile females, 4 newborn males, 1 newborn female and 3 unsexed newborns, for a total of 81 individuals in the Niger herd. The numbers shifted during the study due to individuals ageing, and births and deaths. During the study, 3 adult males, 1 juvenile male and 2 newborn males died. There were 32 births during the same period.

We observed significant spatial sexual segregation within the herd. In the IM, 75% of all adults observed feeding ( $n = 36$ ) were females. In contrast, in the DB, 70% of all observed feeding adults ( $n = 47$ ) were males (Fisher's exact test,  $P < 0.0001$ ). Confirming this bias, 65% of the total bouts of female feeding ( $n = 92$ ) occurred in the IM, while 80% of adult male feeding bouts ( $n = 130$ ) occurred in the DB (Fisher's exact test,  $P < 0.0001$ ).

Pregnancy and reproductive stage were significantly associated with habitat type. Sixty-four percent of the females seen in the DB ( $n = 25$ ) were pregnant and

accompanied by a juvenile offspring. Only 11% of the females in the IM were pregnant with juvenile offspring ( $n = 71$ , Fisher's exact test,  $P < 0.0001$ ). In contrast, 42% of observed females in the IM were accompanied by newborn offspring and females with newborns were never observed in the DB (Fisher's exact test,  $P < 0.001$ ). Pregnant females without offspring made up 18% of those in the IM and 12% of those in the DB. These percentages were identical for adult females accompanied by juvenile offspring and who were not pregnant. Ten percent of the adult females in the IM, and 12% in the DB, were neither pregnant nor had juvenile or newborn offspring.

Species name	Weighted abundance of stems	True abundance of stems	True stem abundance in IM zone	True stem abundance in DB zone
<i>A. digitata</i>	9	3	2	1
<i>A. indica</i>	2	1	–	1
<i>A. macrostycha</i>	2	1	1	–
<i>A. nilotica</i>	4	3	–	3
<i>A. senegal</i>	–	–	–	–
<i>A. senegalensis</i>	155	155	89	66
<i>A. seyal</i>	12	12	–	12
<i>A. siebriana</i>	–	–	–	0
<i>B. aegyptica</i>	168	128	83	45
<i>B. parkii</i>	–	–	–	–
<i>B. rufescens</i>	13	11	9	2
<i>C. aculeatum</i>	19	19	1	18
<i>C. africana</i>	–	–	–	–
<i>C. glutinosum</i>	50	36	30	6
<i>C. nigricans</i>	–	–	–	–
<i>C. occidentalis</i>	–	–	–	–
<i>C. procera</i>	15	14	8	6
<i>C. zambisicus</i>	–	–	–	–
<i>D. mespiliformis</i>	3	1	–	1
<i>F. albida</i>	141	105	17	88
<i>F. gnaphalocarpa</i>	–	–	–	–
<i>F. platyphylla</i>	3	1	–	1
<i>G. senegalensis</i>	641	591	548	43
<i>Gardenia</i> sp.	–	–	–	–
<i>H. thebaica</i>	104	104	–	104
<i>M. crassifolia</i>	1	1	–	1
<i>M. inermis</i>	13	7	–	7
<i>P. africana</i>	16	6	4	2
<i>P. juliaflora</i>	–	–	–	–
<i>P. macrophylla</i>	29	17	7	10
<i>P. reticulatum</i>	52	52	35	17
<i>S. birrea</i>	16	8	2	6
<i>T. avicennioides</i>	5	2	2	–
<i>T. indica</i>	12	6	–	6
<i>Z. mauritiana</i>	14	12	1	11

**Table 2** Data from vegetation surveys conducted in the dry-season habitat of *G.c.peralta* in Niger

### Vegetation surveys

The weighted versus unweighted (simple stem counts) vegetation estimates yielded few differences in the relative abundance of the plant species encountered in the surveys (Table 2), so we used the simple stem counts for our analyses. We recorded a total of 16 species in the IM, with *Guiera senegalensis* being by far the dominant species (Table 2). In contrast, more species (23) were recorded in the DB, but their abundance was more evenly distributed (Table 2).

### Feeding preferences

When sex, age and zone were ignored, giraffes showed the strongest preference (i.e. fed the longest relative to stem abundance) for *Acacia nilotica*, *Acacia seyal* and *Combretum glutinosum*, and the strongest avoidance of *G. senegalensis*, *Annona senegalensis* and *Hyphaene thebaica* (Table 3). A strong preference index for *C. glutinosum* was apparent in the IM (Table 4). It was followed by relatively lower strengths of preference for *Faidherbia albida* and *Acacia senegal*. When each sex's preferences are examined, this trend disappears (Table 4). Both sexes showed a strong preference for *C. glutinosum*, but the similarity ends there. The males' secondary preferences for *Prosopis africana* and *A. nilotica* were relatively strong, while the females' overwhelming preference for *C. glutinosum* was followed by weaker secondary preferences (Table 4). Both subadult males (61% of their total diet) and subadult females (58% of their total diet) spent an inordinate proportion of time eating *P. africana* in the IM. The relative strengths of avoidance changed little across sex or age.

In the DB, the herd showed overwhelming preference indices for *A. nilotica* and *A. seyal* (Table 5). The strongest avoidance scores in this zone included *H. thebaica* and *A. senegalensis*. Both *Balanites aegyptica* and *F. albida* were avoided, which contrasts with the preference shown for these species in the IM. Separately, both males and females still showed a strong preference for *A. nilotica* and *A. seyal* (Table 5), with males having a slightly greater preference for *A. seyal* than females. These two species of tree provided the majority of the giraffes' diet in this region, despite their low occurrence rates in the landscape (Table 2). The preference and avoidance indices did not change with age. Giraffes used plant parts other than leaves from 11 different species. For some

**Table 3** Feeding preference indices for *G.c. peralta* in the dry-season habitat of Niger

Plant species	Preference index ranks in dry-season habitat for <i>G.c. peralta</i>
<i>Acacia nilotica</i>	0.2407
<i>Acacia seyal</i>	0.2072
<i>Combretum glutinosum</i>	0.1329
<i>Acacia senegal</i>	0.0506
<i>Faidherbia albida</i>	0.0389
<i>Acacia siebriana</i>	0.032
<i>Prosopis africana</i>	0.0269
<i>Ficus gnaphalocarpa</i>	0.0174
<i>Maerua crassifolia</i>	0.0163
<i>Ficus platyphylla</i>	0.0077
<i>Ziziphus mauritiana</i>	0.0071
<i>Gardenia sp.</i>	0.0051
<i>Prosopis juliaflora</i>	0.0027
<i>Cassia occidentalis</i>	0.0018
<i>Butyrospermum parkii</i>	0.0013
<i>Commiphora africana</i>	0.0006
<i>Croton zambisicus</i>	0.0005
<i>Combretum nigricans</i>	0.0004
<i>Diospyros mespiliformis</i>	0.0002
<i>Azadirachta indica</i>	-0.0008
<i>Adansonia digitata</i>	-0.001
<i>Terminalia avicennioides</i>	-0.0015
<i>Tamarindus indica</i>	-0.0046
<i>Mitragyna inermis</i>	-0.0054
<i>Sclerocarya birrea</i>	-0.0062
<i>Buhinia rufescens</i>	-0.0084
<i>Calotropis procera</i>	-0.0108
<i>Parinari macrophylla</i>	-0.0115
<i>Combretum aculeatum</i>	-0.0147
<i>Balanites aegyptica</i>	-0.0346
<i>Piliostigma reticulatum</i>	-0.0349
<i>Hyphaene thebaica</i>	-0.0802
<i>Annona senegalensis</i>	-0.119
<i>Guiera senegalensis</i>	-0.4559

plants, only the flowers were used, for others multiple plant parts were eaten (Table 6). This non-leaf forage base included species with both high and low preference indices.

### Other important plant species

The most important shade tree used by giraffes was *Parinari macrophylla*, with 57% of the 65 events observed. *F. albida* was used for shade during 9 (14%) observations. Other shade trees used included *P. africana*, *F. platyphylla*, *C. glutinosum*, *A. seyal*, *B. aegyptica* and *Diospyros*

Species	Preference index for <i>G.c. peralta</i> in the intermediate zone	Preference index for females in the intermediate zone	Preference index for males in the intermediate zone
<i>C. glutinosum</i>	0.4243	0.4578	0.3238
<i>F. albida</i>	0.0902	0.0956	0.0738
<i>A. senegalensis</i>	0.0886	-0.1061	-0.099
<i>P. africana</i>	0.0731	0.0473	0.1505
<i>M. crassifolia</i>	0.0518	0.069	0
<i>Z. mauritiana</i>	0.0483	0.0477	0.0503
<i>A. senegal</i>	0.0329	0.1101	0.0241
<i>A. siebriana</i>	0.0232	0	0
<i>Gardenia</i> sp.	0.0033	0	0.0133
<i>C. nigricans</i>	0.0013	0.0018	0
<i>C. occidentalis</i>	0.0002	0	0.001
<i>A. indica</i>	0	0	0
<i>B. aegyptica</i>	0	-0.0113	0.0288
<i>B. rufescens</i>	0	-0.0107	-0.0107
<i>C. zambisicus</i>	0	0	0
<i>D. mespiliformis</i>	0	0	0
<i>F. gnaphalocarpa</i>	0	0	0
<i>F. platyphylla</i>	0	0	0
<i>H. thebaica</i>	0	0	0
<i>M. inermis</i>	0	0	0
<i>P. juliaflora</i>	0	0	0
<i>T. indica</i>	0	0	0
<i>A. nilotica</i>	-0.0012	0.0022	0.1248
<i>B. parkii</i>	-0.0012	0	0
<i>C. africana</i>	-0.0012	0	0
<i>A. digitata</i>	-0.0024	-0.0024	-0.0024
<i>S. birrea</i>	-0.0024	-0.0024	-0.0024
<i>T. avicennioides</i>	-0.0024	-0.0024	-0.0024
<i>P. macrophylla</i>	-0.0083	-0.0083	-0.0083
<i>C. procera</i>	-0.0095	-0.0095	-0.0095
<i>C. aculeatum</i>	-0.0107	-0.0012	-0.0012
<i>P. reticulatum</i>	-0.0408	-0.0404	-0.0417
<i>A. seyal</i>	-0.1043	0.0171	0.0417
<i>G. senegalensis</i>	-0.6528	-0.6527	-0.6532

**Table 4** Feeding preference indices for *G.c. peralta* in the intermediate zone in Niger

*mespiliformis*. Of 15 observations of giraffes 'scratching' themselves on trees, 8 (53%) used *P. macrophylla*.

## Discussion

### Sexual segregation

**Habitat segregation.** The majority of hypotheses on sexual segregation in ungulates apply to species that have defined rutting seasons and thus temporary segregation periods, or they aim to explain the departure of males to poorer quality ranges. Main & Coblentz (1990) suggested that males altruistically leave superior ranges, minimiz-

ing foraging competition with their mates and offspring. We can reject this hypothesis in the case of the Niger population, because the males actually seemed to be on the better range. The browse in the DB tends to be higher in fats, moisture and carbohydrates, while being lower in ash content than the browse in the IM (Table 1). This range also contains the only open water in the region, forcing the females to make a daily or twice-daily trek from the IM to the DB to drink.

The second hypothesis cited by Main & Coblentz (1990) was male predator avoidance owing to the stresses of reproduction. A third posits that segregation may minimize sexual competition and aggressive behaviour

**Table 5** Feeding preference indices for *G. c. peralta* in the Dollo Bosso in Niger

Species	Preference index for <i>G. c. peralta</i> in the Dollo Bosso	Preference index for females in the Dollo Bosso	Preference index for males in the Dollo Bosso
<i>A. senegal</i>	0.3402	0.0314	0.0319
<i>A. siebriana</i>	0.2857	0.0047	0.0601
<i>B. aegyptica</i>	0.0477	-0.0207	-0.0596
<i>A. senegalensis</i>	0.0318	-0.1444	-0.1444
<i>F. platyphylla</i>	0.0261	-0.0022	0.0141
<i>G. senegalensis</i>	0.0105	-0.0941	-0.0941
<i>Gardenia</i> sp.	0.0059	0.0115	0.0044
<i>P. africana</i>	0.0042	-0.0044	0.0067
<i>P. juliaflora</i>	0.0041	0	0.0052
<i>C. procera</i>	0.0025	-0.0131	-0.0131
<i>B. rufescens</i>	0.002	-0.0044	-0.0042
<i>C. glutinosum</i>	0.0009	0.0405	-0.0119
<i>D. mespiliformis</i>	0.0007	0.0043	-0.0022
<i>A. nilotica</i>	0	0.3518	0.3368
<i>C. occidentalis</i>	0	0	0.0032
<i>T. avicennioides</i>	0	0	0
<i>A. digitata</i>	-0.0003	-0.0022	0.0003
<i>C. nigricans</i>	-0.0003	0	0
<i>F. albida</i>	-0.0007	-0.0976	-0.0595
<i>A. indica</i>	-0.0022	-0.0022	-0.0022
<i>M. crassifolia</i>	-0.0022	-0.0022	-0.0022
<i>C. aculeatum</i>	-0.0042	-0.0394	-0.0394
<i>C. zambisicus</i>	-0.0131	0	0.001
<i>S. birrea</i>	-0.0131	-0.0131	-0.0131
<i>T. indica</i>	-0.0131	-0.0131	-0.0131
<i>M. inermis</i>	-0.0153	-0.0153	-0.0153
<i>P. macrophylla</i>	-0.0194	-0.0204	-0.0191
<i>Z. mauritiana</i>	-0.0241	-0.0241	-0.0241
<i>P. reticulatum</i>	-0.0299	-0.0189	-0.0331
<i>C. africana</i>	-0.0394	0	0.0011
<i>B. parkii</i>	-0.0509	0	0.0026
<i>F. gnaphalocarpa</i>	-0.0679	0.0717	0.013
<i>A. seyal</i>	-0.1444	0.2434	0.2977
<i>H. thebaica</i>	-0.2276	-0.2276	-0.2276

in the nonbreeding seasons. We can reject both, because the Niger giraffes have no defined breeding season and male–male competition occurs year round. In addition, segregation in our population is not complete.

A fourth hypothesis (Main & Coblentz, 1990) was that males may depart to more open ranges in order to avoid damage to their antlers, while still maintaining dominance hierarchies. In contrast, in giraffes both sexes have horns and our males occur in more densely forested areas than the bulk of the females. Foster (1966), Ginnett & Dennent (1997), Pellew (1984), and Young & Isbell (1991) have documented males in denser cover than females in several herds of giraffes in east Africa.

Main & Coblentz (1990) cited a final hypothesis that males may optimize forage resources and females trade off foraging benefits for habitats that are more suitable for raising young. We believe that this best explains our data. We propose that the avoidance of the DB by cows with newborns serves to protect their young in two ways: (i) it avoids food inimical to nursing their young (see dietary segregation), and (ii) it minimizes contact with potential predators when accompanied by more vulnerable newborns.

The entire range of the *G. c. peralta* is free from all predators, with the exception of humans. The IM has a low human population, with few villages and almost zero

Tree species	Leaves	Bark	Flowers	New shoots	Seeds
<i>A. senegal</i>	92%	—	—	8%	—
<i>A. sieberiana</i>	75%	—	25%	—	—
<i>A. nilotica</i>	83%	12%	2%	—	3%
<i>B. aegyptica</i>	92%	8%	—	—	—
<i>C. glutinosum</i>	93%	—	2%	5%	—
<i>C. occidentalis</i>	50%	50%	—	—	—
<i>F. albida</i>	95%	2%	—	3%	—
<i>F. platyfolia</i>	21%	79%	—	—	—
<i>G. senegalensis</i>	—	—	100%	—	—
<i>M. crassifolia</i>	—	—	100%	—	—
<i>P. africana</i>	70%	30%	—	—	—

\*If trees are not listed then leaves comprised 100% of observed forage.

**Table 6** Percentage of browse intake for different parts of the tree species when averaged over the entire herd of *G.c. peralta* in their dry-season habitat in Niger

farming activity during the dry season. Thus, cows with newborns can easily avoid human contact by staying in the IM. The DB, on the other hand, is densely populated. Farming in this region occurs year round with unavoidable human contact. We did not have one observation period in the DB without seeing other people. Additionally, many dunes and depressions in the landscape reduce the long distance visibility that giraffes rely upon for protection from predators (Pellew, 1984; Young & Isbell, 1991).

**Dietary segregation.** The preference for *P. africana* in the IM can be attributed entirely to subadults. This strong selection by subadults for *P. africana* (61% of males' and 58% of females' observed diets) may be due to the high fat and low ash content (Table 1). The bark, which makes up 30% of the intake from *P. africana*, contains moderate levels of tannin relative to the adult's preferred, but tannin rich, *A. nilotica* (Table 5). Males showed a strong preference for *A. nilotica* and *A. seyal* in the DB, both of which are high in protein (Table 1). They exhibit a preference for *C. glutinosum* in the IM, much as the females do, but not as strongly. Unlike the females, males retain their preference for *A. nilotica* in the IM, although this species is exceedingly scarce there. For the females, this secondary preference rank is filled by *A. senegal*. *A. senegal* is no more abundant in the IM than is *A. nilotica*, but it is much higher in protein (28.6%) and moisture (61%), both of which are in low supply in their most preferred species, *C. glutinosum* (Table 1). *C. glutinosum* actually has the lowest protein and moisture contents of all the preferred species (10% protein and 5.04% moisture).

Thus, females may be supplementing their diets with *A. senegal* in order to make up for this deficiency.

If this is true, why are females selecting *C. glutinosum* when in the IM? Since both *Acacia* species are higher in fats, protein and moisture and much lower in ash than *C. glutinosum* they should be preferred. The reverse preference may be attributed to *C. glutinosum*'s relative abundance, high carbohydrate content or potentially low tannin content. We can eliminate the abundance hypothesis because *G. senegalensis*, *B. aegyptica* and *A. senegalensis* are all much more abundant in the IM. Both *G. senegalensis* and *B. aegyptica* are comparable to *C. glutinosum* in the composition of their leaves in every category except the fat content for *G. senegalensis*, which is very low (0.18%). This fact allows us to eliminate the possibility that females are simply seeking browse with a high carbohydrate content. Pellew (1984) suggested that females seek a high-energy browse and avoid browse with a high fibre content in the dry season.

This leaves us with the hypothesis that the females in the IM are avoiding tannins. The pods of *A. nilotica* contain about 30% tannin and those of *A. seyal* contain about 20%. While the specific tannin levels in *C. glutinosum* and *A. senegal* are unknown, *Acacias* in general have higher tannin levels than *Combretums* (Sauer, 1983). *A. senegal* does not have high enough tannin levels to be used as commercially as *A. nilotica* and *A. seyal* are. This may explain the selection differences between the males and females in the IM. Although there is no information on the tannin content of *C. glutinosum*, we can provide circumstantial evidence to support this hypothesis.



Females in the DB, like males, exhibit strong preferences for both *A. nilotica* and *A. seyal*. However, females in the IM show weak preferences for both of these species, while the males still seek out *A. nilotica*. Young & Isbell (1991) also noted this shift in female feeding and the consistency of the males' preferences when in different vegetation zones in Kenya. They concluded that this was because of a difference in habitat preference. We disagree that this was caused solely by habitat selection. When we take into account the fact that nursing cows never come into the DB, and that the majority of cows that do come in are pregnant, this trend begins to make sense in terms of dietary and not just habitat preference. Nursing cows may be avoiding tannins because they are not palatable to their young when passed on through the milk. Pregnant cows, having high energy requirements, would benefit from the higher quality forage of the *Acacias* available in the DB. *A. nilotica* is higher in fats and proteins than *C. glutinosum* (Table 1). *Acacia* species are also lower in ash content than are the *Combretum* species (Sauer, 1983).

The strongest avoidance ( $< -0.1$  preference index) by both sexes was identical in rank for both zones. This avoidance pattern indicates that these plants make poor quality forage. In the DB, *H. thebaica* was the most strongly avoided species. We saw no instances of giraffes browsing on *H. thebaica*, even though it is the most abundant species in this region. *Hyphaene* spp., being monocotyledons, are extremely fibrous and therefore most likely unpalatable to browsers. This species is also avoided by the domestic livestock of the region, further supporting its' being unpalatable to ungulates.

The second most avoided species in both the DB and the IM was *A. senegalensis*. This is a shrubby plant, rarely reaching more than 1 m high, which may contribute to its avoidance rank. There must be more involved in this avoidance than size alone, since giraffes have been reported to eat low lying bean plants. Thus, if this plant was attractive enough, the size and trouble involved in eating it would not be enough to deter them. As McNaughton & Georgiadis (1986) suggested, there may be nutritional imbalances in some plants that act as a defence against herbivory, with no deleterious effects to the plants themselves. It is quite possible that an imbalance of this type occurs here. A further discussion of this avoidance would be speculation, as there are no data available on the plant's composition.

The third strongest avoidance differs between males and females, with males avoiding *G. senegalensis*, and females avoiding *F. albida*. However, the rank of *F. albida* ( $-0.0976$ ) is almost tied with *G. senegalensis* ( $-0.0941$ ) for the females. Possibly the slight difference in ranks is caused by the large stature (often  $> 20$  m tall) of *F. albida*. The lowest branches of these trees were often above the feeding height of the females in the DB. In the IM it is consumed much more frequently by both sexes. This may be due to the lack of other *Mimosaceae* species in this zone, or because the *F. albida* in the IM are generally much smaller. Although giraffes in neither zone display a preference for this species, it is actually utilized frequently, and it is the abundance of the tree that drives the preference index ranks down. This avoidance rank should not be confused with a total avoidance of this species. On the contrary, *F. albida* comprised over 60% of the observed diet of juvenile females in the IM.

Although similar to *C. glutinosum* in composition, we only observed the very abundant *G. senegalensis* being eaten once, and even then, only the flowers for 13 s. The dry weight composition data for this species tells us little about why it might be avoided. Some of the traditional uses of the plant may shed light on the matter, as multiple medicinal uses of the leaves of *G. senegalensis* are well known in Niger. In powder form the leaves are used to treat everything from severe cuts and burns to internal disorders, and to stimulate lactation in both humans and livestock. Whatever chemicals are at play here may cause avoidance by the giraffes.

Ngog Nej (1984) and Mohamed (1995) provide the only prior studies on giraffe diet in west Africa. Both list *B. aegyptica* among the most preferred tree species by giraffes. Our results differ. Although the giraffes consumed this species, they demonstrate an avoidance of it in the DB and a weak preference in the IM. Even in the IM, where *B. aegyptica* was consumed regularly, it comprised less than 20% of the adult's observed diets and less than 10% for subadults and juveniles. Foster (1966) suggested that giraffes in the Serengeti National Park pass up *Balanites* species for more preferred food species. Obviously, this is also the case in Niger. *B. aegyptica* is one of the most abundant species in both regions. It is much more abundant than any of the preferred species in either region. The composition of this plant is higher in protein (14.24%) than any of the preferred species (with the exception of *A. senegal*), however, it is low in fats and relatively low in moisture (0.82% fats and 4.16% moisture).

One could speculate that this is a case of the natural defences of this species at work. *B. aegyptica* has very large spines on the branches (up to 8 cm long). Nevertheless, after many observations of the giraffes eating both the leaves and the thorns, we would have to reject this possibility. Knowing that the *G.c. peralta* in Waza National Park, Cameroon, do indeed show a preference for this species (Ngog Nej, 1984), and are moderate consumers in Niger, we can eliminate the possibility that this tree has a strong chemical deterrent, as may be the case with *G. senegalensis*. Thus, we must assume that giraffes can differentiate between the seemingly slight differences in composition between this species and *C. glutinosum*.

## Conclusion

Unlike the findings of Bleich, Bowyer & Wehausen (1997) and McCullough, Hirth & Newhouse (1989) for other ungulates, the results of this study indicate that the habitat choice exhibited by female giraffes in Niger may be driven more by nutritional demands than by an avoidance of predators or resource partitioning. The apparent avoidance of high levels of tannins by nursing females requires them to pass up the otherwise high quality forage preferred by the males in the DB and only return to it when they have finished lactating.

## References

- BARBOUR, M.G., BURK, J.H. & PITTS, W.D. (1980) *Terrestrial Plant Ecology*. Benjamin/Cummings Publications, California, USA.
- BLEICH, V.C., BOWYER, R.T. & WEHAUSEN, J.D. (1997) Sexual segregation in Mountain Sheep: Resources or predation? *Wildl. Monogr.* **134**, 1–50.
- BOOTH, F.E.M. & WICKENS, G.E. (1988) *Non-Timber Uses of Selected Arid Zone Trees and Shrubs in Africa*. FAO of the UN, Rome, Italy.
- CIOFOLO, I. (1995) West Africa's last giraffes: the conflict between development and conservation. *J. Trop. Ecol.* **11**, 577–588.
- DAGG, A.I. & FOSTER, J.B. (1976) *The Giraffe: Its Biology, Behavior, and Ecology*. Robert E. Krieger Publications Co, Florida, USA.
- FOSTER, J.B. (1966) The giraffe of Nairobi National Park: home range, sex ratios, the herd, and food. *E. Afr. Wildl. J.* **4**, 139–148.
- GINNETT, T.F. & DENNENT, M.W. (1997) Sex differences in giraffe foraging behavior at two spatial scales. *Oecologia* **110**, 291–300.
- IRVINE, F.R. (1961) *Woody Plants of Ghana*. Oxford University Press, London, UK.
- LE PENDU, Y. & CIOFOLO, I. (1999) Seasonal movements of giraffes in Niger. *J. Trop. Ecol.* **15**, 341–253.
- MAIN, M.B. & COBLENTZ, B.E. (1990) Sexual segregation among ungulates: a critique. *Wildl. Soc. Bull.* **18**, 204–210.
- VON MAYDELL, H.J. (1983) *Arbes et Arbustes Du Sahel. Leurs Caracteristiques et Leurs Utilisations*. GTZ, Eschborn.
- MCCULLOUGH, D.R., HIRTH, D.H. & NEWHOUSE, S.J. (1989) Resource partitioning between sexes in white-tailed deer. *J. Wildl. Manage.* **53**, 277–283.
- MCCNAUGHTON, S.J. & GEORGIADIS, N. (1986) Ecology of African grazing and browsing mammals. *Annu. Rev. Ecol. Syst.* **17**, 39–65.
- MOHAMED, M. (1995) Ecological considerations for the management of giraffes and its implications for tourism: a case study of Koure-Boboye area in Niger Republic. Unpublished Thesis, University of Ibadan, Ibadan, Nigeria.
- NGOG NEJ, J. (1984) Regime alimentaire de la girafe au Parc National de Waza, Cameroun. *Mammalia* **48**, 173–184.
- PELLEW, R.A. (1984) The feeding ecology of a selective browser, the giraffe (*Giraffa Camelopardalis Tippelskirchi*). *J. Zool. Lond.* **202**, 57–81.
- SAUER, J.J.C. (1983) A comparison between *Acacia* and *Combretum* leaves utilized by giraffe. *S. Afr. J. Anim. Sci.* **13**, 43–44.
- YOUNG, T.P. & ISBELL, L.A. (1991) Sex differences in giraffe feeding ecology: energetic and social constraints. *Ethology* **87**, 79–89.

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